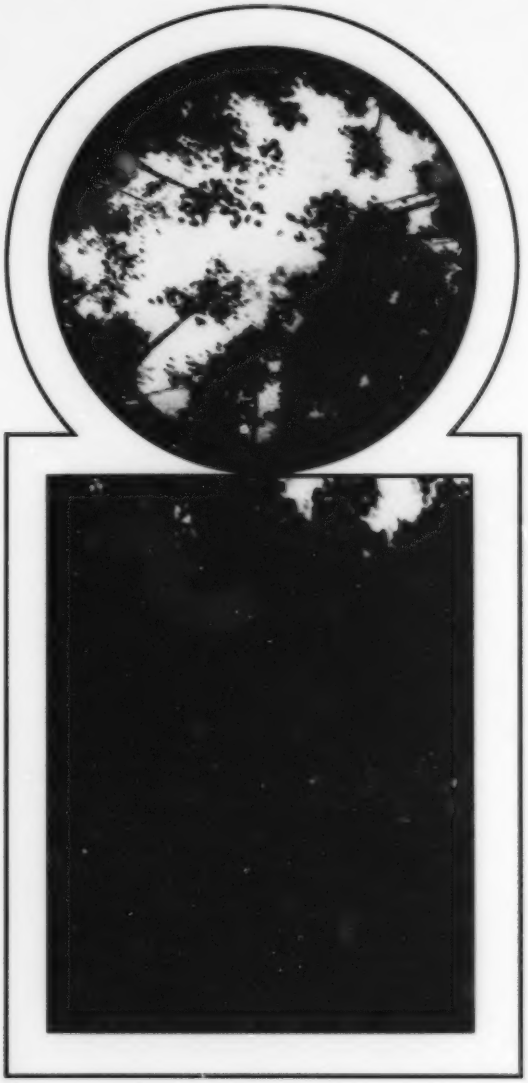
Forest Research Report No. 126

# A Comparison of New Proximity-based Expressions of Competing Vegetation



Ontario
Ministry of
Natural
Resources

**Cover Photos:**

**Overhead competition from non-crop perennial vegetation reduces seedling survival and growth in Northern Ontario plantations.**

# A Comparison of New Proximity-based Expressions of Competing Vegetation

Blake MacDonald

Ontario Forest Research Institute
1235 Queen Street East
P.O. Box 969
Sault Ste. Marie, Ontario
P6A 5N5

Ontario
Ministry of
Natural
Resources

**Canadian Cataloguing in Publication Data**

MacDonald, G. Blake
A comparison of new proximity-based expressions of competing vegetation

(Forest research report, ISSN 0381-3924 ; 126)
ISBN 0-7729-9105-7

1. Competition (Biology).
I. Ontario Forest Research Institute.
II. Title.
III. Series.

QH546.3M32 1991 574.5'247 C92-092500-6

© 1991, Queen's Printer for Ontario
Printed in Ontario, Canada

Single copies of this publication are available at no charge from the address noted below. Bulk orders may involve charges.

Ministry of Natural Resources
Ontario Forest Research Institute
P.O. Box 969
Sault Ste. Marie, Ontario
P6A 5N5

Telephone: (705) 946-2981
Fax: (705) 946-2030

Cette publication scientifique n'est disponible qu'en anglais.

92-06036/

## TABLE OF CONTENTS

ABSTRACT ..... ii

INTRODUCTION ..... 1

METHODS ..... 2
Field and laboratory ..... 2
Index formulation and statistical analyses ..... 3

RESULTS AND DISCUSSION ..... 6

CONCLUSIONS ..... 12

ACKNOWLEDGMENTS ..... 13

REFERENCES ..... 13

MacDonald, G.B. 1991. A comparison of new proximity-based expressions of competing vegetation. Ontario Ministry of Natural Resources, Forest Research Report No. 126. 17 p.

## ABSTRACT

Indices of interspecific competition from perennial vegetation were formulated and tested for their ability to explain variation in the diameter increment of black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings. The indices were derived from either vertical hemispherical photographs or field measurements. They differed with respect to the number and proximity of the surrounding competitors included. The optimum index was calculated as the amount of competing canopy on a vertical hemispherical photograph in relation to the seedling leaf area. This index explained up to 75% of the variation in seedling root collar diameter increment. An alternative index that also performed well was the sum of the relative competing stem volumes based on one dominant competitor in each quadrant surrounding the seedling. This index explained up to 62% of the variation in diameter growth. The proposed single-term indices are convenient for functional growth analysis, and applicable to container and bare-root stock of both black spruce and jack pine. Adoption of large competition radii and exclusion of small competitors are recommended for indices designed to assess competition from perennial non-crop species in young conifer plantations.

## INTRODUCTION

Unacceptable mortality and growth loss of young conifer seedlings resulting from vegetative competition have been reported throughout North America (Eis 1981, Oxenham 1983, Knapp *et al.* 1984, McDonald and Oliver 1984, Oliver 1984, Fox 1986, Brace and Bella 1988). The adverse effects are largely attributable to competition for the light, moisture and nutrients required for the growth of crop trees (Radosevich and Osteryoung 1987). Competition problems are intensified by silvicultural measures that oppose natural successional trends. For example, planting conifers on sites that are naturally regenerating to fast-growing angiosperms such as trembling aspen (*Populus tremuloides* Michx.) necessitates considerable effort to maintain crop dominance. Accurate measures of competition from undesirable species are essential to enable silviculturists to prescribe the most effective timing and intensity of release treatments.

Competition indices are commonly designed to assess intraspecific interference in mature stands (Cottam and Curtis 1956, Mead 1966, Gerrard 1969, Bella 1971, Keister 1971, Moore *et al.* 1973, Lorimer 1983, Cannell *et al.* 1984). Recently, some indices have been developed to quantify interspecific competition in young plantations (Howard and Newton 1984, Brand 1986, Wagner and Radosevich 1991). Such indices are valuable for assessing the free-to-grow status of young stands and for planning effective strategies for removing competitors.

This study addresses the effects of the abundance and proximity of competition from non-crop perennials on the performance of planted black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings. Perennial competitors are a serious threat to plantation productivity on upland sites, which can be completely dominated by suckers of trembling aspen soon after harvesting (Pollard 1971). Both container and bare-root stock of each species are included because physiological differences after outplanting have been reported between the stock types (Blake and Sutton 1987).

The objective of the present study was to formulate a monomial (single-term) index of perennial vegetative competition, using distance-based criteria for the inclusion of competitors. A monomial expression for competition was sought to facilitate the calculation of relative growth rates in future studies. Simplicity of formulation and applicability to all species and stock types were considered to be desirable features of the index because they would make it acceptable for operational assessment of competition in young plantations.

## METHODS

### *Field and laboratory*

Twelve operational plantations were sampled following their fourth growing season. Three plantations were selected from each of four stock types: (1) overwintered black spruce paperpot container stock, (2) 1½ + 1½ black spruce bare-root stock, (3) overwintered jack pine paperpot container stock, and (4) 2 + 0 jack pine bare-root stock. The plantations were on clearcut and scarified boreal mixedwood sites in Ontario, located between 48°32'N and 49°53'N latitude and between 85°10'W and 92°15'W longitude. The topographies were flat, and the soils ranged in texture from coarse sand to clay.

Each plantation contained a wide range of competition intensity. The main tree species were trembling aspen, white birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.f.). Competing shrubs included beaked hazel (*Corylus cornuta* Marsh.), speckled alder (*Alnus rugosa* (Du Roi) Spreng.), red maple (*Acer rubrum* L.), and choke cherry (*Prunus virginiana* L.).

Sixty seedlings were randomly sampled in each plantation. Field measurements were conducted between mid-July and mid-September, after most of the height growth and foliar development had been completed for the seedlings and competitors. Competing perennial stems within a 140-cm radius of the seedling were measured for total height and root collar diameter. To eliminate the unnecessary measurement of large numbers of remote small stems, competitors were included only if their height exceeded a 45° vertical angle subtended at the base of the seedling. The distance and azimuth were also measured between the root collar of each competitor so identified and that of the seedling. A hemispherical photograph of the overhead canopy was taken with a Minolta 7.5-mm equidistant fisheye lens from the base of the seedling's leader. A range pole placed due east of the seedling provided directional reference. The total canopy area on each hemispherical photograph was measured with an electronic planimeter. It should be noted that all perceptible foliage on each photograph was measured, including that of competitors beyond the 140-cm plot radius.

The seedling in each plot was destructively sampled after budset in mid-September. Needles were removed for determination of fresh leaf areas from the uppermost lateral branches, using 200 needles per seedling for black spruce and 100 needles for jack pine. The total height was recorded, current-year shoots were clipped, and a basal disk was removed for growth-ring analysis. The projected area of the fresh needle sample was measured with a Li-Cor 3100 area meter after photocopying the

needles onto transparencies, and the oven-dry mass of the needles was determined (drying for 48 hours at 70°C). The current-year leaf area was calculated by multiplying the total oven-dry mass of current foliage by the ratio of leaf area to dry mass from the needle subsample. The total diameter and current diameter increment were measured on each basal disk.

### *Index formulation and statistical analyses*

A previous study of the same plantations separated the effects of seedling size, soil factors and competition on seedling growth (MacDonald *et al.* 1990). It was recommended that an index should express the amount of competition in relation to the seedling size and should include both horizontal and vertical components of competition. An index of competitor dominance status relative to the crop is more useful for field assessment of the need for release than is an index of the absolute amount of competition with no reference to the seedlings.

In this study, an index based on the hemispherical photographs was formulated according to the above principles. It was expressed as:

$$[1] \qquad CR = CAN/LAS$$

where CR is the relative competing canopy, CAN is the total canopy area ($cm^2$) measured on the hemispherical photographs, and LAS is the projected area ($cm^2$) of current-year seedling foliage. The placement of the camera at the base of the seedling's leader made CR a relative index in the vertical dimension. The divisor (LAS) was included to relate the seedling and competitors with respect to the horizontal extents of their foliage. The remaining indices were variations of the following expression:

$$[2] \qquad VR = [\Sigma(B_i \bullet H_i)]/(B_s \bullet H_s)$$

where VR is the relative competing stem volume, $B_i$ is the root collar basal area of competitor i, $H_i$ is the height of competitor i, $B_s$ is the root collar basal area of the seedling and $H_s$ is the height of the seedling. Although the neighboring stem volumes would provide negligible competitive effect, it was assumed that VR indirectly quantified the dimensions of crowns and roots. The variations of this index differed only with respect to the rule for competitor selection. Competitors were chosen by hemisphere, quadrant or annulus around the seedling, as defined for each index in

Table 1.

The number of competitors included in the expressions varied from two (VRH) to unlimited (CR), and the maximum potential competitor distance ranged from 50 cm (VR50) to infinity (CR). The relative performance of these expressions would identify the important criteria for the inclusion of neighbors in an effective competition index.

Current root collar diameter increment was used to assess seedling response to competition for all species and stock types. This approach is justified because higher levels of resources are required to support cambial growth than apical growth (Lanner 1985). Thus, diameter increment should be more responsive than height increment to competition-related resource deficiencies. Relative growth measures are often necessary to eliminate the influence of a subject tree's initial size on growth (Ledig 1974). However, unmodified diameter growth is a valid response variable because it qualifies as a geometrically unbiased specific increment (Duff and Nolan 1957).

Seedling growth reduction caused by dense competition could be counteracted by a corresponding positive site effect. This may occur if site productivity is correlated with both seedling growth and competition intensity. However, an earlier study (MacDonald *et al.* 1990) indicated that the influence of soil quality on seedling growth was unimportant compared with the influences of competition level and seedling size.

Scatterplots revealed a curvilinear relationship between seedling growth and the competition indices. The following exponential function was hypothesized:

$$[3] \qquad Y = e^{bX^c}$$

where Y is the seedling diameter growth and X is the competition index. Many natural processes, such as forest growth and canopy light penetration, are based on the exponential function (Horn 1971, Gellert *et al.* 1975). The natural logarithmic transformation was applied twice to the data prior to least-squares regression (Dowdy and Wearden 1983). The transformation required the omission of seedlings with competition index values of zero to avoid undefined logarithms. Plots of residual errors indicated that linearization and variance stabilization had been achieved by the transformation. A separate linear regression was conducted for each species, stock type and competition index, using SAS statistical software (SAS Institute Inc. 1988).

TABLE 1. Criteria for selecting competitors in the proposed expressions of vegetative competition.

| Index | Competitors included |
|---|---|
| CR | Unobscured portions of all competitors as recorded on a vertical hemispherical photograph, with no constraint on distance from seedling. |
| VR140 | All competitors within a 140-cm radius around seedling. |
| VRH | Largest competitor[a] in east hemisphere and largest competitor[a] in west hemisphere, within a 140-cm radius around seedling. |
| VRQ | Largest competitor[a] in each of the northeast, southeast, northwest and southwest quadrants, within a 140-cm radius around seedling. |
| VR50 | All competitors within a 50-cm radius around seedling. |
| VR100 | All competitors within a 100-cm radius around seedling. |
| VRMID | All competitors in the middle annulus (50.1 to 100 cm from seedling). |
| VROUT | All competitors in the outermost annulus (100.1 to 140 cm from seedling). |

[a]Based on vertical angle from seedling root collar to competitor apex, calculated from competitor height and distance to seedling.

## RESULTS AND DISCUSSION

The survival and growth of crop trees is limited by the availability of light, moisture, nutrients and physical space. However, since light intensity is commonly a critical factor for young plantations (Strothmann 1967, Kellomäki *et al.* 1979, Reed *et al.* 1983, Strong and La Roi 1983, Brand 1986), the assessment of aboveground competition was emphasized in this study. The effects of shoot and root competition cannot be effectively separated because rapid shoot growth (the prerequisite for aboveground competitive superiority) is dependent upon high rates of uptake of water and nutrients by roots (Grime 1977, Horn 1971). Fitter and Hay (1981) recognized the synergism between the effects of root and shoot competition, and concluded that competitive superiority in plants is largely a function of the ability to overshadow the leaves of neighbouring plants. Competition for soil nutrients may be important in conifer plantations on some sites (Brand and Janas 1988), but such competition is assessed and controlled by aboveground measurements and silvicultural operations.

Goldberg and Fleetwood (1987) reported that the effect of competition on annual species was strongly nonlinear, with a large growth reduction resulting from a few competitors followed by smaller effects from additional competitors. Similar nonlinear trends were evident in the present study for all the species and stock types sampled. The patterns for black spruce container stock are shown as examples in Figures 1 and 2.

The fact that each additional unit of competition had a smaller negative effect on seedling growth than the preceding unit may be explained by the increasing mutual interference with resource-gathering among surrounding competitors. The diminishing seedling response may be accentuated by physiological and morphological adaptations of crop tree foliage under heavy shade, which offset decreases in the rate of photosynthesis (Brix 1967, Boardman 1977, Fitter and Hay 1981).

In the present study the F-ratios for all linear regressions were significant at $P=0.001$. The regression statistics are presented in Tables 2 and 3. The relative competing canopy (CR) generally produced the highest coefficient of determination and the lowest error mean square. Whereas the other indices quantified light interception indirectly, CR accurately expressed the extent of radiation interference perceived by the seedling. The photographic index was unconstrained by an arbitrary plot radius, and it automatically assigned reduced weight to competitors that were distant or obscured by intervening vegetation. It measured the potential for carbon fixation, and hence for cambial growth, by relating the amount of competing foliage to the current foliage of the seedling.

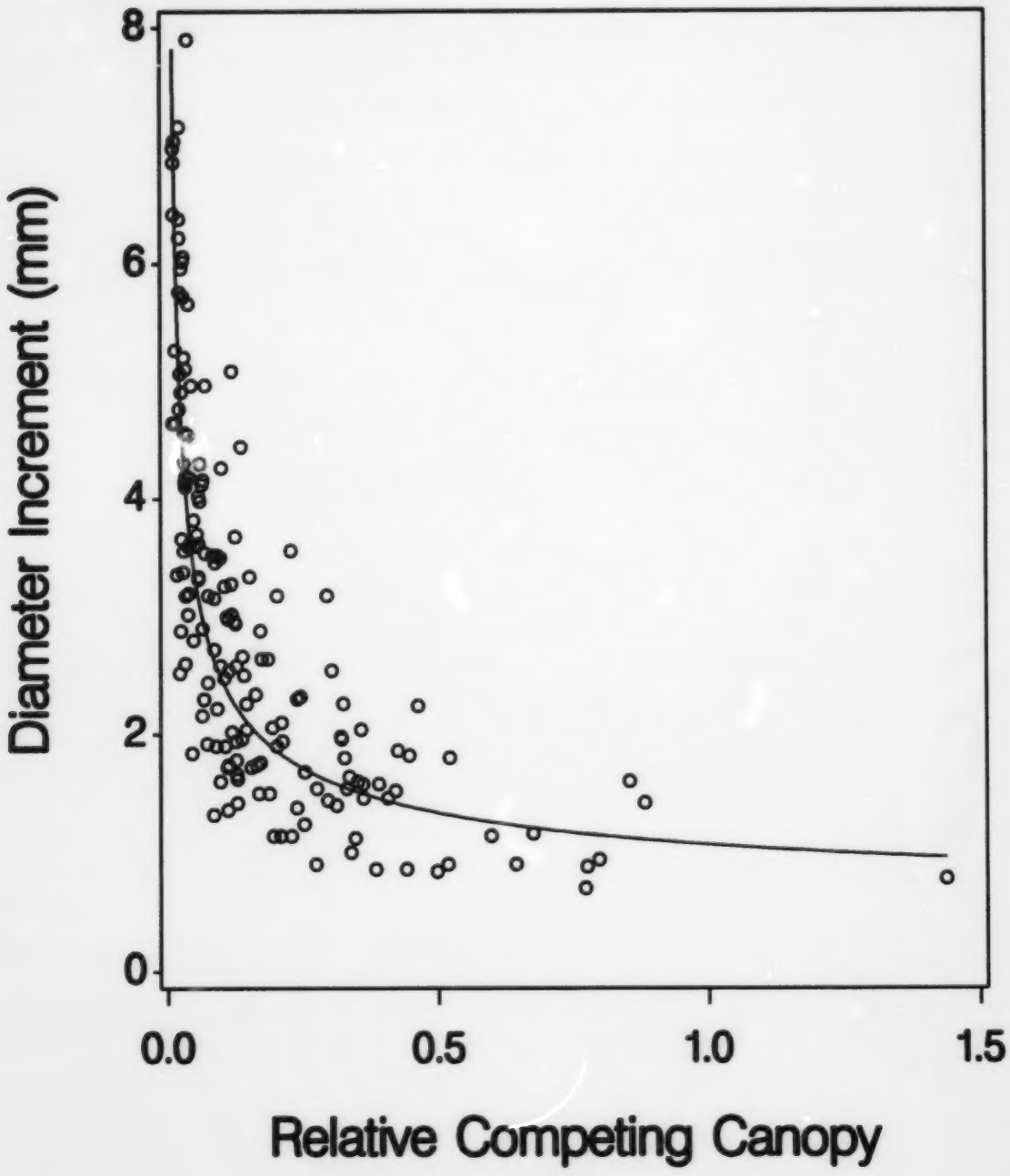



FIGURE 1. Exponential model for the relationship between diameter increment and relative competing canopy (CR) for black spruce container stock.

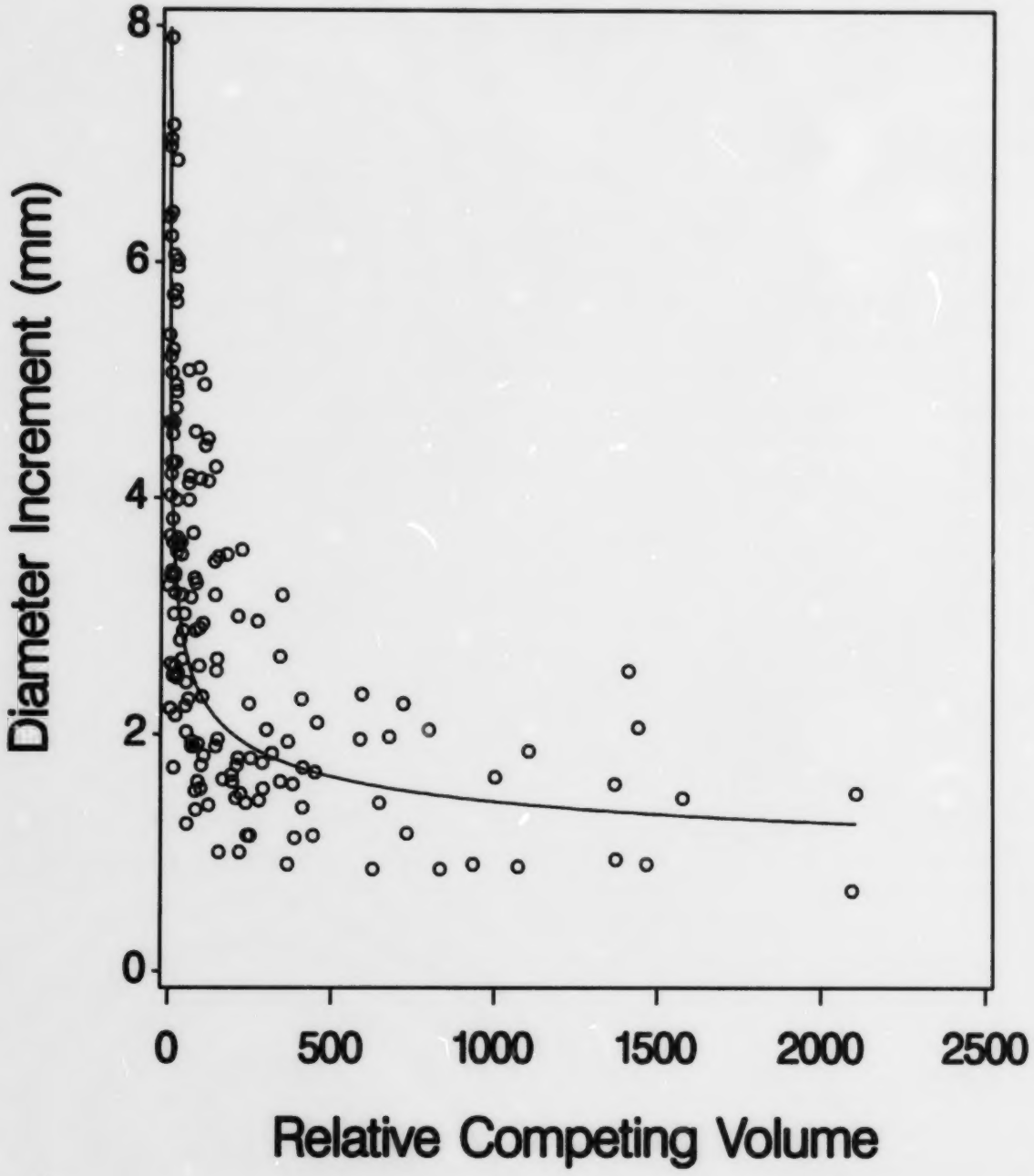



FIGURE 2. Exponential model for the relationship between diameter increment and relative competing volume (VRQ) for black spruce container stock.

TABLE 2. Regression statistics[a] for the relationships between seedling diameter increment and all competition indices for black spruce.

| | Container stock | | | | | Bare-root stock | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Coefficients[b] | | | | | Coefficients[b] | |
| Index | n[c] | $r^2$ | MSE | b | c | n[c] | $r^2$ | MSE | b | c |
| CR | 166 | 0.69 | 0.9894 | 2.3664 | -0.1314 | 171 | 0.29 | 1.9137 | 2.4094 | -0.1118 |
| VR140 | 161 | 0.57 | 2.5806 | 4.5500 | -0.0668 | 167 | 0.30 | 1.9898 | 4.1085 | -0.0450 |
| VRH | 162 | 0.50 | 2.3036 | 4.1957 | -0.0667 | 167 | 0.30 | 1.8950 | 3.9608 | -0.0513 |
| VRQ | 162 | 0.56 | 2.4262 | 4.4163 | -0.0733 | 167 | 0.32 | 1.9508 | 4.0639 | -0.0519 |
| VR50 | 105 | 0.42 | 1.4071 | 3.5609 | -0.0439 | 130 | 0.06 | 1.8775 | 3.3861 | -0.0109 |
| VR100 | 156 | 0.44 | 2.0911 | 3.9811 | -0.0506 | 165 | 0.16 | 2.0557 | 3.7094 | -0.0299 |
| VRMID | 149 | 0.35 | 1.9631 | 3.8776 | -0.0477 | 163 | 0.21 | 2.0202 | 3.7841 | -0.0367 |
| VROUT | 154 | 0.46 | 1.3608 | 4.1622 | -0.0608 | 162 | 0.30 | 1.6980 | 3.9182 | -0.0429 |

[a]Values for $r^2$ (coefficient of determination) and MSE (error mean square, $mm^2$) are calculated from the original untransformed units.

[b]Function form: $Y = e^{bX^c}$, where Y is the diameter growth ($m \times 10^{-4}$) and X is the competition index.

[c]The sample size (n) was originally 180, but seedlings with missing growth data or with competition index values of zero were omitted.

TABLE 3. Regression statistics[a] for the relationships between seedling diameter increment and all competition indices for jack pine.

| | Container stock | | | | | Bare-root stock | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Coefficients[b] | | | | | Coefficients[b] | |
| Index | n[c] | $r^2$ | MSE | b | c | n[c] | $r^2$ | MSE | b | c |
| CR | 165 | 0.70 | 4.5463 | 3.1248 | -0.0834 | 164 | 0.75 | 2.7710 | 3.3347 | -0.0687 |
| VR140 | 163 | 0.54 | 7.8758 | 4.7284 | -0.0513 | 161 | 0.64 | 4.2390 | 4.7319 | -0.0364 |
| VRH | 165 | 0.50 | 9.3066 | 4.4728 | -0.0579 | 159 | 0.61 | 4.2908 | 4.5799 | -0.0386 |
| VRQ | 166 | 0.53 | 8.0829 | 4.5966 | -0.0587 | 158 | 0.62 | 4.1944 | 4.6231 | -0.0371 |
| VR50 | 134 | 0.51 | 5.2617 | 4.1135 | -0.0445 | 120 | 0.51 | 3.9319 | 4.2235 | -0.0281 |
| VR100 | 156 | 0.47 | 7.3789 | 4.4924 | -0.0480 | 159 | 0.62 | 3.9719 | 4.5260 | -0.0321 |
| VRMID | 153 | 0.45 | 8.0032 | 4.4738 | -0.0494 | 155 | 0.58 | 4.2481 | 4.4754 | -0.0312 |
| VROUT | 160 | 0.56 | 8.4115 | 4.5602 | -0.0522 | 155 | 0.52 | 4.9221 | 4.5450 | -0.0320 |

[a]Values for $r^2$ (coefficient of determination) and MSE (error mean square, $mm^2$) are calculated from the original untransformed units.

[b]Function form: $Y = e^{bX^c}$, where Y is the diameter growth ($m \times 10^{-4}$) and X is the competition index.

[c]The sample size (n) was originally 180, but seedlings with missing growth data or with competition index values of zero were omitted.

An alternative to CR would be required in situations where data from hemispherical photographs were unavailable. The relative competing volume within a radius of 140 cm from the seedling (VR140) generally explained more growth variation than the other relative volume indices (Tables 2 and 3). However, VRH and VRQ had similar regression statistics and may be preferable in practice. Only two competitors and four competitors had to be measured for VRH and VRQ, respectively, whereas approximately 20 competitors were required to calculate VR140. VRQ is recommended over VRH on the basis of its higher coefficients of determination.

The range in performance of the indices demonstrated the importance of the technique used for competitor selection in formulating an index. It appears that remote woody perennials, including those more distant than the height of the seedling, have a significant competitive effect. The optimum index (CR) included the most distant competitors, some of which were well beyond the 140-cm plot radius. A comparison of the performances of VR50, VR100 and VR140 (Tables 2 and 3) reveals that increased $r^2$ values generally resulted from enlarging the competition radius. In every case, the competitors in the outer annulus (VROUT) explained more growth variation than the competitors in the innermost annulus (VR50).

A fixed competition radius has the disadvantage of including small trees with minor competitive effects, and excluding large trees that may interfere with resource availability. This problem would be more pronounced in stands with complex structures than in uniform monocultures. The superior performance of CR may be attributable both to its variable competition radius and to its ability to account for partial blocking of competitors by intervening trees.

In some plantations, an improvement in index performance may be expected by selecting competitors on the basis of a minimum horizontal angle (Daniels 1976), or by subtracting the relative sizes of suppressed neighbours from the overall index (Tomé and Burkhart 1989). Such guidelines were supported in this study by the success of VRH and VRQ. These indices used vertical angles rather than distances to select competitors, ignoring small trees near the subject seedlings.

Remote competitors are not significant for some old-field herbaceous species (Goldberg 1987), or for intraspecific competition in monocultures of Scots pine (*Pinus sylvestris* L.) (Pukkala and Kolström 1987), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) or lodgepole pine (*Pinus contorta* Dougl.) (Cannell *et al.* 1984). However, the present study has shown that distant hardwood competitors can be important in young conifer plantations. The contrast with the results of the previously cited studies may be explained by the greater plasticity and efficiency of angiosperm crowns compared with gymnosperm crowns (Bond 1989). A competitive effect may be exerted by the

diversion of moisture and nutrients by the fine roots of distant competitors that enter a seedling's rhizosphere. Thus, spot weeding by removing competitors within a small radius may be inadequate for complete release of crop trees in some plantations.

This study compared several expressions of competition at only one point in time (four years after plantation establishment). Potential changes in the physiology and allometry of the seedlings and competitors could result in different rankings of the competition indices at other developmental stages.

## CONCLUSIONS

Previous results from the same plantations revealed that competition for light, as measured on hemispherical photographs, is an effective index of vegetative competition (MacDonald *et al.* 1990). It was subsequently shown that an index derived from hemispherical photographs is superior to indices based on mensurational data for predicting seedling size (Morris and MacDonald 1991). The present study demonstrates that the inclusion of competitor proximity affects the performance of indices formulated from mensurational data. However, the photographic index remains a better predictor of diameter growth for container and bare-root stock of black spruce and jack pine.

The relative competing canopy (CR) is recommended as the optimum index tested. It quantifies photosynthetic potential more accurately than the other indices, but requires a fisheye lens and leaf area meter for component measurements. The sum of the relative competing volumes of the largest competitor in each quadrant surrounding the seedling (VRQ) performs well and requires no elaborate equipment. It is recommended as a simple index for field assessment.

The important components of competition must be combined multiplicatively rather than additively if a single-term index is required. This was accomplished for the indices in this study by using a product form to combine the horizontal and vertical dimensions of competition (equation 2), and a quotient form to express the amount of competition relative to the size of the seedling (equations 1 and 2).

It appears that significant negative influence is exerted by interspecific competition located far from a seedling. Small competitors close to a seedling may be less important than dominant trees at greater distances.

## ACKNOWLEDGMENTS

This study was funded as part of project no. 33506 under the Canada-Ontario Forest Resource Development Agreement. Valuable assistance was provided by Dave Morris, Steven Hills and Robert Forslund.

## REFERENCES

Bella, I.E. 1971. A new competition model for individual trees. For. Sci. 17: 364-372.

Blake, T.J. and Sutton, R.F. 1987. Variation in water relations of black spruce stock types planted in Ontario. Tree Physiol. 3: 331-344.

Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28: 355-377.

Bond, W.J. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biol. J. Linn. Soc. 36: 227-249.

Brace, L.G. and Bella, I.E. 1988. Understanding the understory: dilemma and opportunity. *In* Management and Utilization of Northern Mixedwoods. Edited by J.K. Samoil. Can. For. Serv. Inf. Rep. NOR-X-296. 163 p.

Brand, D.G. 1986. A competition index for predicting the vigour of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. 16: 23-29.

Brand, D.G. and Janas, P.S. 1988. Growth and acclimation of planted white pine and white spruce seedlings in response to environmental conditions. Can. J. For. Res. 18: 320-329.

Brix, H. 1967. An analysis of dry matter production of Douglas-fir seedlings in relation to temperature and light intensity. Can. J. Bot. 45: 2063-2072.

Cannell, M.G.R., Rothery, P. and Ford, E.D. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. 53: 349-362.

Cottam, G. and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. 22: 454-456.

Dowdy, S. and Wearden, S. 1983. Statistics for research. John Wiley and Sons, N.Y. 537 p.

Duff, G.H. and Nolan, N.J. 1957. Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in *Pinus resinosa* Ait. Can. J. Bot. 35: 527-572.

Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce. Can. J. For. Res. 11: 1-8.

Fitter, A.H. and Hay, R.K.M. 1981. Environmental physiology of plants. Academic Press, London. 355 p.

Fox, T.R. 1986. Raspberry (*Rubus idaeus* L.) competition effects on balsam fir (*Abies balsamea* (L.) Mill.) seedlings in northern Maine. Tree Planters' Notes 37(2): 20-23.

Gellert, W., Küstner, H., Hellwich, M., and Kästner, H. 1975. The VNR concise encyclopedia of mathematics. Van Nostrand Reinhold Co., N.Y. 760 p.

Gerrard, D.J. 1969. Competition quotient: a new measure of the competition affecting individual forest trees. Michigan State Univ., East Lansing, Agric. Exp. Stn. Res. Bull. 20. 32 p.

Goldberg, D.E. 1987. Neighborhood competition in an old-field plant community. Ecology 68: 1211-1223.

Goldberg, D.E. and Fleetwood, L. 1987. Competitive effect and response in four annual plants. J. Ecol. 75: 1131-1143.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Natur. 111: 1169-1194.

Horn, H.S. 1971. The adaptive geometry of trees. Princeton Univ. Press, Princeton, N.J. 144 p.

Howard, K.M. and Newton, M. 1984. Overtopping by successional Coast-Range vegetation slows Douglas-fir seedlings. J. For. 82: 178-180.

Keister, T.D. 1971. A measure of the intraspecific competition experienced by an individual tree in a planted stand. Louisiana State Univ., Baton Rouge, Agric. Exp. Stn. Res. Bull. No. 652. 30 p.

Kellomäki, S., Salminen, R., Hari, P., Ventilä, M., Kanninen, M., Kauppi, P. and Smolander, H. 1979. A method for approximating the photosynthetic production of stand members inside the canopy. J. Appl. Ecol. 16: 243-252.

Knapp, W.H., Turpin, T.C. and Beuter, J.H. 1984. Vegetation control for Douglas-fir regeneration on the Siuslaw National Forest: a decision analysis. J. For. 82: 168-173.

Lanner, R.M. 1985. On the insensitivity of height growth to spacing. For. Ecol. Manage. 13: 143-148.

Ledig, F.T. 1974. Concepts of growth analysis. *In* Proc. 3rd North American Forest Biology Workshop. Edited by C.P.P. Reid and G.H Fechner. College of Forestry and Natural Resources, Colorado State Univ., Fort Collins, CO. 388 p.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. 6: 343-360.

MacDonald, G.B., Morris, D.M. and Marshall, P.L. 1990. Assessing components of competition indices for young boreal plantations. Can. J. For. Res. 20: 1060-1068.

McDonald, P.M. and Oliver, W.W. 1984. Woody shrubs retard growth of ponderosa pine seedlings and saplings. *In* Proc. 5th Annual Forest Vegetation Management Conference, Sacramento, CA. USDA For. Serv., Pacific Southwest Forest and Range Exp. Stn., Redding, CA. pp. 65-89.

Mead, R. 1966. A relationship between individual plant-spacing and yield. Ann. Bot. 30: 301-309.

Moore, J.A., Budelsky, C.A. and Schlesinger, R.C. 1973. A new index representing individual tree competitive status. Can. J. For. Res. 3: 495-500.

Morris, D.M. and MacDonald, G.B. 1991. Development of a competition index for young conifer plantations established on boreal mixedwood sites. For. Chron. 67: 403-410.

Oliver, W.W. 1984. Brush reduces growth of thinned ponderosa pine in northern California. USDA For. Serv. Res. Pap. PSW-172. 7 p.

Oxenham, R. 1983. A study on the effect of competing vegetation and browsing on early plantation performance. Nova Scotia Dep. Lands and Forests Forest Technical Note No. 5. 9 p.

Pollard, D.F.W. 1971. Mortality and annual changes in distribution of above-ground biomass in an aspen sucker stand. Can. J. For. Res. 1: 262-266.

Pukkala, T. and Kolström, T. 1987. Competition indices and the prediction of radial growth in Scots pine. Silva Fenn. 21: 55-67.

Radosevich, S.R. and Osteryoung, K. 1987. Principles governing plant-environment interactions. *In* Forest vegetation management for conifer production. Edited by J.D. Walstad and P.J. Kuch. John Wiley & Sons, N.Y. pp. 105-156.

Reed, K.C., Shumway, J.S., Walker, R.B. and Bledsoe, C.S. 1983. Evaluation of the interaction of two environmental factors affecting Douglas-fir seedling growth: light and nitrogen. For. Sci. 29: 193-203.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, NC. 1028 p.

Strong, W.L. and La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. 13: 1164-1173.

Strothmann, R.O. 1967. The influence of light and moisture on the growth of red pine seedlings in Minnesota. For. Sci. 13: 182-191.

Tomé, M. and Burkhart, H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. 35: 816-831.

Wagner, R.G. and Radosevich, S.R. 1991. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. Can. J. For. Res. 21: 821-828.